XXV.—*Brief Observations on the Anatomy of* Comatula. By C. Semper*. *With an Addendum by* W. B. Carpenter, M.D., LL.D., F.R.S., &c.

Since the publication of Müller's celebrated treatise on the structure of *Pentacrinus caput-Medusæ*†, errors have been propagated by all the manuals of zoology (and so-called comparative anatomy), the refutation of which no one, to my knowledge, has hitherto attempted. To me, however, the erroneousness of some individual statements of that great man was already known while residing in the Philippine Islands; and from the commencement of my course as a teacher I have in my lectures endeavoured to spread truer views.

In the year 1868 I was intending to publish a short memoir on that which I had found, when, becoming acquainted in London with Dr. Carpenter, I was delighted to learn that that able observer had obtained exactly the same results on European as I on Philippine *Comatulæ*. In the expectation that the English investigator would soon publish his already prepared work on the Crinoidea, I deferred till now the communication of the results of my examination: but since, after five years waiting, there is imminent risk that from my lectures the results of Carpenter's and my own toilsome investigations may somehow find their way into publicity, I hold that the moment has arrived to break the silence I have hitherto kept.

My present concern is only to correct Müller's inaccurate representation of the sexual parts and what he calls the nervous system. He says (*l. c.* p. 57), "In the arms of *Pentacrinus* and *Comatula*, between the joints and the membranous covering of the groove (derived from the perisome), under the groove of the tentacle are situated two‡ membranous canals, one above the other. *Between the two lies the nerve-cord* of the arm, specially enclosed in a membranous sheath; opposite each pinnule it forms a longish slight swelling from which the nerve-fibre departs into the pinnule." This description has been admitted into Gegenbaur's 'Grundzüge der vergleichenden Anatomie,' 2nd ed. p. 321§, and Claus's 'Zoologie,'

* Translated from a separate impression, communicated by Dr. W. B. Carpenter.

† Abhandlungen der Berlin. Akad. 1841.

‡ This is only partially correct. According to Müller's own drawing (*l. c.* pl. iv. f. 12), *Alecto europæa* has only one canal in the arms; the lower one is absent. In the tropical *Comatulæ*, however, it is present, and also in the European, according to Edmund Perrier (Arch. d. Zool. Expérim. &c. tome ii. 1873, pp. 49, 57). To the work of the latter I shall return further on.

§ I take this opportunity to protest against the mode in which Gegen-

2nd ed. Müller further on (*l. c.* pp. 58, 59) describes the ovaries as lying in the pinnules completely isolated from each other, and compares this situation to that of the analogous organs in the proglottides of the Cestoda.

The cord discovered by Müller (*l. c.* pl. iv. fig. 11, pl. v. f. 16) between the two canals of the arm—which, moreover, is wanting in the drawing of a section of the arm of *Comatula europæa* (*l. c.* pl. iv. f. 12)—is indeed present; it is not, however, the nerve-system, but belongs to the parts of generation. This is proved by sections of the arm of a new *Comatula* from the Philippines, which I shall subsequently describe; the sections were made on arms carefully decalcified. The pinnules, as is well known, arise with a tolerably sharp curve towards the arm. At the period of sexual maturity the ovaries prolong themselves in the same direction into the soft portions of the arm before uniting with each other through the cord (Müller's nervous cord) which runs along the middle line. In transverse sections, therefore, made close behind the insertion of a pinnule, the prolongations of the ovaries which are situated in the hinder part of the arm, under the groove of the tentacle, must be met with, and, in a favourable case, also the cords connecting them with the central cord. Such sections are in fact obtained with tolerable facility. In the annexed woodcut (fig. 1), on the left the pinnule is not met with; but on the right it is, though only partially. In the proper body-parts of the arm, under the tentacle-canal *c.t* (from which the lateral vessels depart for the tentacle) a cord *r*, cut through somewhat obliquely, is seen in the middle line: this is Müller's nerve of the arm (see fig. 2). To the right of it is situated a portion of the right ovary, *ov*, with developed ova mostly on

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baur quotes from my Monograph of the *Holothuriæ* in his 'Lehrbuch;' his readers are not informed of the existence of such a work, but only that I published some observations on *Holothuria* in my 'Reisen im Archipel der Philippinen.' I myself can bear the disadvantage thence arising; but it is not so easy for others to do so, because they are led into error by *his* authority. Recently a Privatdocent at Graz has written a special memoir on the histology of the Holothuria, without the slightest suspicion that he could have found all his supposed novelties already in my book. Moreover I cannot suppress the conjecture that Gegenbaur himself has not carefully read my work; otherwise he would hardly have granted a place in his own to manifest errors. For it is not true that (as he says, p. 343 of the 2nd edition of his 'Grundzüge') "neither the structure nor the function of the Cuvierian organs are known." The former is better explained by me than almost any other organ by others; and the negative result of my investigation, that they were certainly not glands, is much more positive than Gegenbaur's absolutely arbitrary assumption that they are "probably excretory organs" (*l. c.* p. 329).

the outer periphery; but here its connexion with the central cord was not brought into view. On the contrary the peripheral layer of the central cord clearly passes into the mass of

Fig. 1.

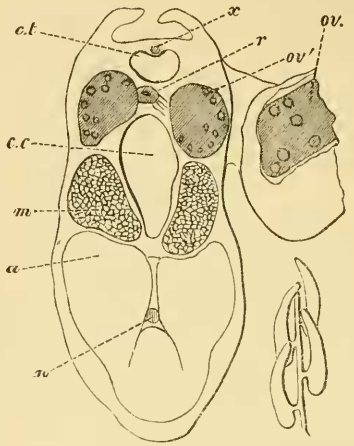

Fig. 2.

Fig. 1. Transverse section of a decalcified Arm: *a*, organic basis of the skeleton; *n*, cord occupying the canal of the calcareous segment, regarded by Müller as a vessel and by Carpenter as a nerve; *m*, muscles; *c.c*, inferior or cœliac canal; *r*, cord regarded by Müller as a nerve, by Carpenter and Semper as the rhachis of the generative system; *ov*, ovary; *c.t*, superior canal, the tentacular canal of Müller: *x*, fibrous cord of Perrier and Semper, corresponding in situation with the real tentacular canal of Carpenter.

the left ovary. The ova here, as well as in the pinnules, show a distinct germ-vesicle and spot. Müller has seen these connecting branches, as is shown in the representation of what he calls the nervous cord (*l. c.* pl. v. f. 16); he interprets them as lateral nerves for the pinnules. Judging from the figure, these branches appear to be very fine; so that, without making sections, Müller might the more readily fail to demonstrate the connexion with the ovaries, as no similar relation in any Echinoderm had given a hint of so peculiar an arrangement of the parts of generation. In what manner these central cords (probably comparable to the rhachis in the ovary of the Nematoda) are distributed in the disk I have not investigated; Müller, however, states, and Carpenter has confirmed it to me, that they are traceable far up the disk and there form a ring round the œsophagus.

The question now is, Where are we to look for the nervous system? In regard to this, unfortunately, my examination has conducted to no conclusion, because I have not yet had any opportunity to repeat it on living animals. It might even be possible that the cord (*n*) in the interior of the calcareous skeleton, which has hitherto always been regarded as a vessel, is a nervous cord; and if so, then the so-called heart situated in the calyx would certainly have to be looked upon as a ganglion. That it is not a vessel, is shown by the total absence of a lumen; its mass consists of very fine close-lying fibres, which Hoffmann also, in his recently published work, compares to nervous fibres. On the other hand, above the tentacle-canal there is a second fibrous cord, which was first discovered by Perrier (Archives de Zoologie Expérimentale, tome ii. 1873, p. 55, pl. iii. f. 8, *m*), and which I have also recognized in sections of the arm of *Comatula* which I have preserved for some years (see *x*, fig. 1). This cord also appears probably to belong to the nervous system. Yet in no case is proof furnished of the nervous nature of either the one or the other; the only thing fully established with respect to the first, is the absence of any ground for interpreting it as a vessel.

In conclusion, I wish to add a remark on the work of Perrier above referred to. He strenuously contends that one of the two canals described by Müller in *Pentacrinus*, and by Carpenter in *Comatula*, is not present, viz. that named by the latter "canalis cœliacus." But in this he to a certain extent contradicts himself. At pp. 48, 49, in directly contesting the presence of the lower canal of the arm, he says:—"for there (in adult individuals) the tentacular canal appears always to *rest directly* upon the *thin layer* of tissues which invests the skeleton, and in that layer *nothing resembling a canal* can be distinguished." In the same page, however, he says "it is upon the walls of the prolongations of the general cavity into the pinnules that the genital glands are developed;" further, p. 57, "the tentacular vessel is seen to rest directly upon the membrane that envelops the calcareous axis;" and, in the same page, "immediately above this covering" (of the calcareous axis) "is the general cavity." A more distinct contradiction cannot be imagined. It seems to me that Perrier has been misled by the German word *Gefäss*. He calls the tentacle-canal a canal, because he wishes to indicate thereby its belonging to a system of vessels distinctly cut off from the body-cavity; while he will not give that name to the canal-like prolongations of the body-cavity (which he yet himself

describes, though not clearly)*, since the body-cavity and consequently also its prolongations are supposed to be separated from the vascular system. His attack on Müller and Carpenter therefore fails, since he finds again the same parts as they, and only arbitrarily changes the name and interpretation. Moreover he is positively behind them both: he denies the existence of the nervous system described by Müller (*l. c.* p. 83); yet it is present, though it was erroneously interpreted by its discoverer. The only really new information given by Perrier is concerning the fibrous band situated above the tentacle-canal (*l. c.* p. 55, pl. iii. f. 8, *m*), with which I am also acquainted, and which, as mentioned above, will probably prove, on closer histological examination of living animals, to be the nervous system that for the moment is yet to be sought.

Addendum by Dr. Carpenter.

The full justice which my friend Prof. Semper has obviously desired to do me, in speaking of my conclusions in regard to the structure of *Comatula*, as having been arrived at independently of, and contemporaneously with, his own, might seem to render it quite unnecessary for me to put forward any claim to a discovery which has, I think, many bearings of great interest, physiological as well as morphological. But he seems to have overlooked the fact that I had not only distinctly pointed out what I believe (in common with him) to be Prof. Müller's errors, but had indicated what I regard as the true Nervous System, in the First part of my "Researches on the Structure, Physiology, and Development of *Comatula rosacea*," communicated to the Royal Society in 1865, and published in the 'Philosophical Transactions' for 1866.

After describing (par. 19) the muscular apparatus of the arms, I say:—"It will be shown, in the Second part of this memoir, that the cord which traverses the length of the arms between the canal just mentioned and another canal which overlies it, and which was regarded by Prof. Müller as a nerve, really belongs to the reproductive apparatus. But it will also be shown that a regular system of branching fibres, proceeding from the solid cord (described by Prof. Müller as a vessel) that traverses the axial canal of each calcareous segment of the rays and arms, is traceable on the extremities of the muscular bundles; and reasons will be given for regarding these fibres as

* This follows indubitably from his remark (p. 49), "the general cavity of the body is continued beneath the tentacular canal."

probably having the functions of nerves, though not exhibiting their characteristic structure."

Again, in describing the dorsal cirrhi (par. 29), the axial canal of the arms (par. 45), and the circlet of basals in the Pentacrinoid larva (par. 76), I mentioned the connexion of these solid sarcodic cords with "the wall of a remarkable quinquelocular organ, contained within the centro-dorsal basin," which organ was "supposed by Prof. Müller, who first noticed its presence [though he did not recognize its subdivision], to be a heart," but which "I shall hereafter describe under the name of the 'centro-dorsal vesicle,' and which I shall show to be an expansion of the original crinoidal axis, hollowed out into a multiple ventricular cavity."

The chief difficulty which I felt in regarding this axis and its extensions into the arms as constituting a Nervous System, arose from the entire absence of any of the ordinary histological characters of nerves. I found that I could tear the axial cords (hardened in strong spirit) into fibrils of extreme minuteness, but that these fibrils showed a perfectly homogeneous composition. Still "the remarkable energy and rapidity of muscular action in *Comatula*, far surpassing that of every other known animal of its class" (par. 19), strongly impressed me with the belief that its muscles must be called into action by nerves proceeding from a common centre; and as these muscles are all *flexors*, while the *extension* of the arms is provided for by elastic ligaments, I arrived at the opinion that the want of histological differentiation in the nervous system might be related to the fact of its having only one kind of action to perform. To this conclusion I have given expression in the last edition of my 'Microscope and its Revelations,' p. 771.

Being at Oban in the summer of 1867, I made an experiment on the living *Comatula*, which seemed conclusive (not only to myself, but to the numerous Physiologists to whom I have mentioned it) as to the nervous character of the central quinquelocular organ and of the cords proceeding from it. Having turned out from the calyx the whole visceral mass (which, in the living animal, is so loosely held in by the soft perisome as often to be lost in the dredge), I had remaining the entire skeleton, its muscles and ligaments, and the supposed nervous system radiating from the central quinquelocular organ still contained in the cavity of the centro-dorsal plate. On irritating the central organ by a needle passed down through the aperture leading into this cavity from the base of the calyx, all the ten arms suddenly and consentaneously coiled up. On the withdrawal of the needle, the arms gradually straightened

themselves again, and again coiled up as before when the irritation of the central organ was renewed.

The only additional proof derivable from experiment as to the nervous character of this apparatus, would be the production of a similar effect in a single arm by irritating the supposed nerve-cord in its course. But this, through the complete inclusion of the cord in the solid calcareous skeleton of the arm, would scarcely be possible.

As I distinctly remember mentioning this experiment to Prof. Semper when I had the pleasure of a visit from him in 1868, I am rather surprised at his saying that no experimental verification of the doctrine has been obtained. I was, on my part, very glad to learn from him that the histological character of the axial cords of *Comatula* closely corresponds with that of what he felt assured to be the Nervous System of the *Holothurida*, his admirable researches on which group ought to be known to every comparative anatomist.

Nothing but the engrossment of my spare time in the various inquiries that have arisen out of the Deep-Sea researches which I prosecuted in the vacations of 1868 and three following years, has prevented me from publishing long before this the Second part of my Memoir on *Comatula*, for which the essential materials (in the shape of some hundreds of preparations, and a series of most admirable drawings executed by Mr. George West and Mr. A. Hollick) have been in my possession ever since the appearance of the First. These drawings, made from very careful dissections, show that the ovaries (or testes) in the pinnules have exactly the same relation to the so-called nerve-cord of Müller, that the currants on a bunch have to their stalk. I was led to trace this connexion, in the first instance, by finding that the position of the ovary in the pinnule, between its two principal (afferent and efferent) canals, exactly corresponds with that of Müller's nerve-cord (*r* in Prof. Semper's figure) between the two canals *c.t* and *c.c* of the arm. They further show that in *Comatula rosacea* the canal *c.t*, spoken of by Müller as the tentacular canal, has no connexion with the tentacles, and exists equally in the oral pinnules which have no tentacles; whilst the real tentacular canal occupies the position *x* in Prof. Semper's figure*. This

* That there is here, in *Comatula rosacea*, a most distinct *canal*, from which the tubular tentacles originate, is a fact of which I am as certain as I am of any point in the anatomy of this animal. Whether the same may not be the case in Prof. Semper's Philippine *Comatula*, is a question which I would commend to his careful investigation. I have a strong belief that in a sufficiently thin section of a pinnule he would find his so-called "fibrous cord" to possess a lumen; though this may be obscured by the collapse of the canal, which is not cylindrical but flattened.

fact also I have indicated in Par. 15 of the First part of my Memoir.

I expect to be able to prove that the *Crinoidea* have scarcely any thing in common with Echinoderms generally as to plan of structure, and that their developmental history differs essentially from that which is now regarded as characteristic of that group. In fact, as Prof. Semper remarked to me, a Crinoid might almost be considered a more highly organized Polype. In its early state the digestive cavity has but a single orifice in the centre of the oral disk; and the animal then exhibits *an absolutely perfect radial symmetry*. The only departure from this symmetry in the adult Crinoid arises from the elongation of the digestive cavity into an intestine, the anal termination of which appears on the oral disk, bearing in *Comatula* an unsymmetrical plate, which belongs to the "perisomatic skeleton"*. The "radial skeleton," with its ligaments, muscles, and nerves, and the complicated vascular, respiratory, and generative systems contained in the arms, all have such an exact radial symmetry, that to affirm that Crinoids are modified Annelidans, merely because the "pro-embryo" which carries about the true Crinoid-germ has somewhat of an Annelid form, seems to me about as scientific as it would be to describe Man as a Radiate, because the villous chorion, which furnishes nutriment to the true Vertebrate embryo, is globular. If the type of the Nervous System goes for any thing, and this nervous system in *Comatula* is what I affirm it to be, its disposition, from its very first appearance, is as distinctly *radiate*, as the disposition of the nervous system in the Articulate and Vertebrate subkingdoms is *bilaterally* symmetrical.

Doubtless I shall be charged in this instance, as I have been in others, with an undue preference for older to newer ideas, and with an indisposition to avail myself of the light thrown by developmental history upon the affinities of animals. I only ask, however, a suspension of judgment until I shall have published the facts which have been in my possession for more than ten years past, and which I only want an interval of leisure concentrated upon the subject to present in a complete and systematized form.

* See par. 84 of the first part of my "Researches."